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AN ABSTRACT OF A THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN PLANT PATHOLOGY
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ACKNOWLEDGMENT

The author takes this opportunity to express his sincere appreciation to Doctor N. B. Linn for his interest and guidance in this work. It is also a pleasure to thank Professor N. E. Stevens and Professor H. W. Anderson for friendly counsel and assistance during the course of graduate studies.

[Reprinted from PHYTOPATHOLOGY, March, 1948, Vol. XXXVIII, No. 3, pp. 235–246.]

INFECTION OF TOMATO FRUITS BY COLLETOTRICHUM PHOMOIDES[1]

JOSEPH P. FULTON[2]

(Accepted for publication November 21, 1947)

The fungus *Colletotrichum phomoides* (Sacc.) Chester has long been considered a wound pathogen on ripe tomatoes. Arthur (1), Chester (2, 3, 4), Halsted (9), Gueguen (8), and others were able to transmit the disease from one ripe tomato to another only by wounding the inoculated fruits. Davidson (5) concluded from field observations that natural infection must take place through microscopic cracks in the cuticle of the fruits. Doolittle (6, p. 27) stated that *C. phomoides* can infect apparently unwounded tomatoes. This statement was based on studies in which healthy tomatoes were sprayed with a suspension of spores of the anthracnose fungus.[3]

Tomato anthracnose develops ordinarily on ripe fruits but the failure to control the disease by application of fungicides to near-ripe or ripe fruits suggests that infection takes place some time prior to ripening (16, 17).

A study was made of some of the factors related to infection of tomato fruits by *Colletotrichum phomoides,* with emphasis on the mode of infection and the stages of maturity at which the fruits are susceptible to infection.

METHODS

Experiments were conducted on greenhouse-grown tomatoes using two red-fruited varieties, Early Baltimore and Garden State. In preliminary studies field-grown tomatoes proved unsatisfactory because of the high percentage of natural infection. The greenhouse plants were started in pots and after several weeks were transplanted to the bench, where they were supported by heavy twine and pruned to two branches. A date tag was attached to each blossom shortly after pollination when the ovaries became slightly swollen.

The inoculum used was obtained from five-day-old cultures of *Colletotrichum phomoides* on potato-dextrose agar slants. A small amount of water was added to each slant and a spore suspension prepared by gently scraping the surface with a wire loop. Spores were then washed[4] by cen-

[1] Condensed from a thesis submitted in partial fulfillment of the requirements for a degree of Doctor of Philosophy in the Graduate School of the University of Illinois.

[2] The writer is indebted to Dr. M. B. Linn for advice during the progress of the work and criticism of the manuscript. Grateful acknowledgement for criticism of the manuscript is also made to Professor N. E. Stevens.

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[4] Washing of the spore suspension was essential especially when green tomatoes were inoculated. Unwashed spore suspensions or agar discs on which the fungus was growing contained materials which diffused from the inoculum into the green fruits causing black spotting and, later, distortion of the fruits.

trifuging through two changes of water. Several ml. of this suspension were poured onto pads of moist cotton approximately two inches in diameter and these were applied to the fruit surfaces. Detached fruits were placed in moist chambers for two days. Fruits inoculated on the vine were covered with waxed paper bags for two days to conserve moisture.

In histological studies of the mode of infection, fruits were inoculated by the methods just described or in some cases with spore suspensions applied in droplets to marked areas on the fruits. Inoculated areas were cut from the fruits at various time-intervals ranging from twenty-four hours to several weeks. The specimens were fixed in FAA, dehydrated in ethyl alcohol, cleared in xylol, and imbedded in paraffin according to the usual methods. Sections were cut 10 microns in thickness and stained with safranin and fast green. A few sections were stained with Flemming's triple stain after decolorizing in Stockwell's solution. Temporary mounts for observation of the spores and appressoria on the fruit surfaces were made by mounting pieces of tomato skin in lacto-phenol containing 0.1 per cent cotton blue.

FRUIT INFECTION

Wounding

In studying the relation of wounding to infection five shallow wounds were made with a sharp needle in the epidermis of each tomato at the time of inoculation. Fruits of various ages were inoculated and allowed to ripen fully on the vines. They were then picked and stored at 80° F. for two weeks. No attempt was made to control humidity. As the lesions appeared care was taken to determine whether the lesions developed from wounds or in the surrounding apparently unwounded areas. The percentages of fruits developing lesions from wounds and the percentage showing lesions in the unwounded areas are presented in table 1.

TABLE 1.—*Infection of wounded tomato fruits*

Variety	Age when inoculated	Number inoculated	Percentage developing lesions from wounds	Percentage developing lesions in unwounded areas
Early Baltimore	10 to 20 days	8	0	50
	20 to 40 days	5	60	80
	40 to 60 days	11	100	72
	Control, uninoculated	16	.....	0
Garden State	10 to 20 days	10	0	70
	20 to 40 days	8	25	87
	40 to 60 days	8	62	100
	Control, uninoculated	15	.....	0

These data indicate that as the fruits approach maturity the pathogen can readily gain entrance through wounds. Young fruits, however, are not easily infected in this manner. Wounding of young fruits causes a corking of the surrounding tissues which effectively prevents further development of the fungus. Wounding, in the manner described, is not necessary to obtain infection. Inoculation of young fruits produces typical lesions only on apparently unwounded areas. Infection of mature fruits can also occur on unwounded areas.

Maturity

The relation of maturity of fruits to the susceptibility to infection by

TABLE 2.—*Infection of unwounded tomato fruits by Colletotrichum phomoides in relation to the age of the fruits when inoculated*

Variety	Age when inoculated	Number inoculated	Percentage of green fruits with stylar rot	Percentage of ripe fruits with typical lesions
Early Baltimore	5 days	8	25	0
	10 days	10	20	0
	15 days	13	7	33[a]
	20 days	14	0	57
	30 days	17	0	88
	40 days	25	0	80
	50 days plus, fruits green	21	0	85
	50 days plus, fruits pink to ripe	15	0	80
	Control, uninoculated	16	0	0
Garden State	5 days	4	75	0
	10 days	13	30	44[a]
	15 days	16	0	62
	20 days	23	0	65
	30 days	11	0	63
	40 days	14	0	85
	50 days plus, fruits green	14	0	92
	50 days plus, fruits pink to ripe	7	0	85
	Control, uninoculated	15	0	0

[a] Calculated on the basis of the fruits which reached maturity.

Colletotrichum phomoides was investigated by inoculating unwounded tomatoes at various ages, viz., 5, 10, 15, 20, 30, 40, 50 days, and later as the fruits colored and ripened. The fruits were picked and stored for two weeks in the same manner as previously described.

The percentages of infection (Table 2) indicate that the fungus can penetrate the cuticle and cause incipient infection at a very early stage in fruit

development. There is some increase in susceptibility to this type of infection as the fruits mature.

A certain number of the fruits inoculated when 15 days old or less developed a stylar rot 20 to 30 days after inoculation. The area around the style became black to dark brown and black sclerotial bodies of the fungus developed in this dry, rotted region. The rot was much more extensive in the interior of the fruits than it was on the exterior. Seeds, as well as the tissues of the walls of the seed cavities, showed discoloration and rotting. *Colletotrichum phomoides* was repeatedly isolated from the affected tissues. Rotting in this instance may have followed injury to the styles at the time of inoculation.

Temperature Relation

Nightingale and Ramsey (13) reported that *Colletotrichum phomoides* was unable to grow on culture media or in wounded tomatoes at temperatures above 95° F. The optimum temperature for growth of the fungus, computed from 6 days' development, was shown to be 80° F. The present work shows that infection of apparently uninjured fruits is obtained over a similar wide range.

Unwounded, ripe tomatoes were inoculated by the method previously described and placed in moist chambers for two days. During inoculation and subsequent storage, fruits were kept at 50, 60, 70, 80, 90, and 100° F. At 50° F. lesions developed slowly after approximately twenty days. Infection was readily obtained at 60 and 70° F., lesions being produced in five to eight days. Most rapid development of lesions was at 80° F. At this temperature they often appeared within three days. Lesions produced at 80° F. and below were similar in appearance to those on field-infected fruits. A few lesions developed at 90° F. after approximately seven days. These few lesions were very small, sunken, and dry. No lesions developed at 100° F.

The time required for the appearance of lesions was not constant for any one temperature. The rapidity with which lesions developed was dependent not only upon temperature but also upon maturity of the fruits at inoculation. Large green tomatoes could be infected in the manner just described but the appearance of the lesions in this case was delayed until after the fruits had ripened.

HISTOLOGICAL STUDIES ON PENETRATION AND INFECTION

Fungi of the genera *Colletotrichum* and *Gloeosporium* characteristically enter the host plant by means of penetration tubes which develop below appressoria. Simmonds (15) studied in detail the penetration of fungi causing the anthracnose diseases of banana, papaw, and mango. In these cases an extremely fine thread develops from a short peg-like projection at the base of the appressorium. The fine thread penetrates the cutin layer and broadens in contact with the cellulose wall of an epidermal cell to form a well-defined hyphal mass between the cutin layer and the cell wall.

Spores of *Colletotrichum phomoides* germinate readily in droplets of water either on tomato fruits or on glass slides. At varying intervals after germination the fungus forms appressoria on the hyphae. On tomato fruits the appressoria may form on the ends of very short hyphae protruding from germinating spores, or they may develop after extensive mycelial growth. Commonly more than one appressorium is formed from a single spore.

Studies of stained sections prepared from inoculated tomatoes show that a penetration tube grows from the lower side of the appressorium into the cuticle (Fig. 1, A, Fig. 2, C, D). This tube is constricted at the point of entry into the cuticle and is swollen midway through the cutin layer. A nucleus is often evident in the penetration tube soon after the tube grows into the cutin layer (Fig. 2, D). Upon contact with the host cell wall the tip of the penetration tube enlarges slightly, pushing the host cell wall inward and away from the cutin layer. These steps in the penetration of the cutin layer have been observed in tomato fruits varying in age from fifteen days to red-ripe maturity.

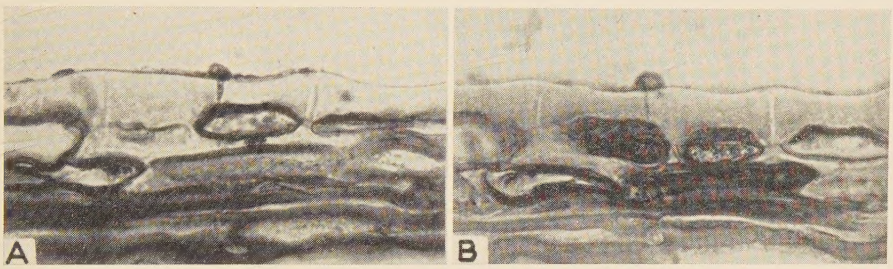

FIG. 1. Penetration beneath appressoria of the cuticle of a Garden State tomato 60 days old, 6 days after inoculation. A. Penetration tube has grown through the cutin layer and is in contact with the epidermal cell wall. B. Fungus hyphae developing from a penetration tube. The hyphae have pushed aside the cell wall and are growing between the cell wall and the cutin layer. The cell contents and the walls and contents of adjacent cells are strongly stained with safranin. Photographs approx. 408 ×.

In green fruits the growth of the pathogen is limited to the area between the cutin layer and cell wall. The cell wall in contact with the penetration tube is heavily stained by safranin. The contents of the affected cell often take the stain more strongly than the adjacent cells. A small swelling in the cell wall usually develops on the side opposite the fungus.

In ripe fruits the hyphae, which have penetrated the cuticle either recently or at some earlier stage when the fruits were green, continue enlargement between the cutin layer and the host cell wall (Fig. 2, E). Lateral development from one epidermal cell to another is apparently prevented by the cutin deposited between the cells. The wall in contact with the fungus is pushed aside by several swollen hyphae. The fungus slowly dissolves the cell wall and the contents are pushed into a small mass at the base which stains with safranin (Fig. 1, B). Adjacent cell walls in the hypodermis and epidermis also show this characteristic staining in advance of the fungus.

From the epidermal cell the fungus grows into the hypodermal layers but never laterally into the adjacent epidermal cells. The development is both inter- and intracellular. When it is intracellular the contents of the cell are pushed aside. The hyphae are swollen, with some constrictions, and limited in extent. At this stage there is a certain amount of lateral development in the hypodermis. The fungus continues to cause discoloration of cell walls and contents in advance of its development.

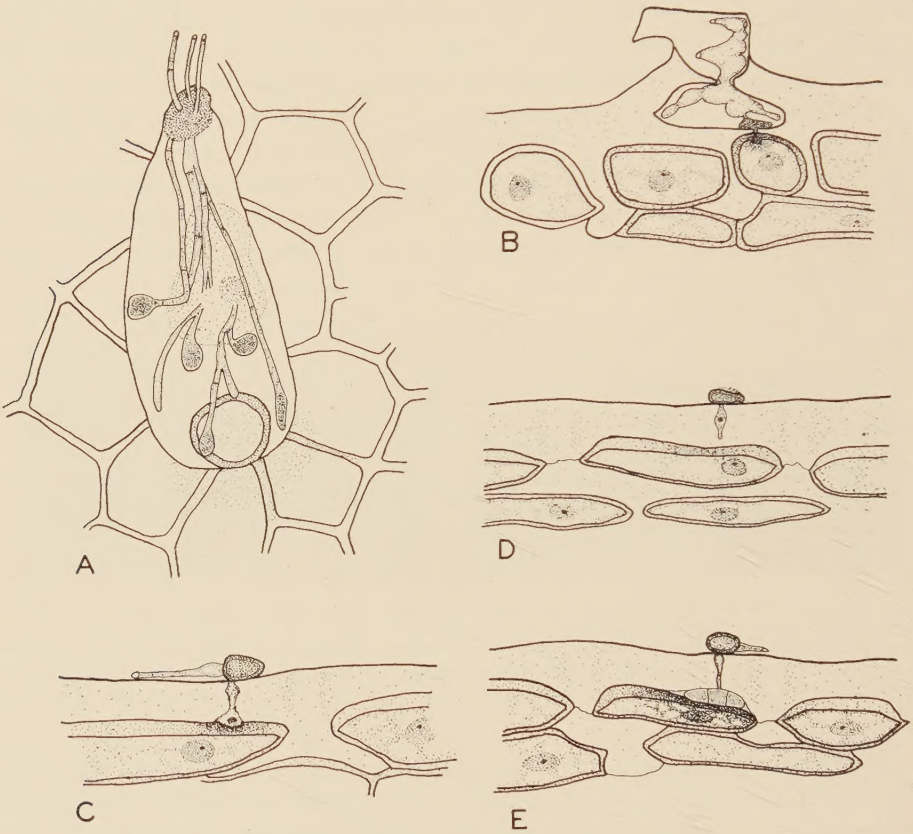

FIG. 2. A. Garden State tomato 28 days old, 2 days after inoculation, showing invasion of broken epidermal hair by hyphae. B. Early Baltimore tomato 33 days old, 4 days after inoculation, showing development of hyphae in epidermal hair and penetration beneath appressorium at base of hair. C. Same tomato showing penetration tube growing through cutin and swelling in contact with cell wall. D. Garden State tomato 60 days old, 6 days after inoculation, showing penetration tube in cutin. E. Same tomato showing swollen hyphae developing between cutin and cell wall. Drawn with aid of camera lucida, approx. 573 ×.

The hyphae change in form and manner of growth when they enter the parenchyma cells below the hypodermal layer. Growth is rapid and more extensive than that observed in the epidermis and hypodermis. The hyphae ramify in all directions showing both intra- and intercellular development. The cell walls and cell contents are penetrated readily and the fungus no longer follows the contours of the cell walls. The hyphae are much finer

than those in the hypodermal layer and are no longer constricted. The cell walls and cell contents are not discolored in response to the fungus. At this stage there is a partial collapse of the cells of the hypodermal layer and the affected parenchyma cells. As the lesion enlarges the fungus continues its development in the parenchyma cells and may also develop laterally in the hypodermal layer and in the cells of the epidermis.

It was noted in temporary mounts of the skin of inoculated fruits that the fungal hyphae were often associated with the epidermal hairs. The fungus penetrated and developed within the cells of some hairs (Fig. 2, A). The hyphae were generally tipped with appressoria near the base of the hair. On ripe fruits lesions occasionally appear to develop from the base of such affected hairs. This penetration and development seems to be essentially the same as that described for cuticular penetration. The fungus forms appressoria at the base of the hair from which it penetrates to adjacent cells of the hypodermal layer (Fig. 2, B). In green fruits the growth of the fungus is arrested at the first cell it contacts beneath the hair. It should be emphasized that the common method of entry of the pathogen is directly through the cuticle, although the epidermal hairs on occasion appear to be infection courts.

Various types of cracks in the cuticle of field-grown tomato fruits have been reported by Young (18) and Groth (7). Davidson (5) has suggested that these are the primary infection courts for *Colletotrichum phomoides*. In the course of the present studies cracks were rarely observed in the cuticle of greenhouse-grown tomatoes. Since the fungus appears to be admirably suited for direct penetration of the cuticle, it is unlikely that cuticular cracks are important in penetration and infection of the fruits.

RELATION OF pH CHANGES IN FRUIT TO GROWTH OF PATHOGEN

One of the striking features of tomato anthracnose is that lesions develop only on ripe or ripening fruits. Since the fungus can exist within or beneath the cutin layer from the time the fruit is 10 days old until maturity, it must be assumed either that there are factors present in green tomatoes which inhibit further development of the fungus or that some material necessary for fungal growth develops during the ripening process. It has been suggested that changes in pH may be a controlling factor. There is no evidence that this is the case.

Nightingale and Ramsey (13), working with tomato anthracnose, concluded that other changes in the fruit during ripening are more important than changes in acidity in influencing the development of decay. They found that the average pH of the green tomatoes which they studied was 4.7 and that of ripe tomatoes 6.01. Their conclusions were based on the growth of *Colletotrichum phomoides* on potato-dextrose agar adjusted to these two values.

Hamner and Maynard (10), reviewing the factors influencing the nutritive value of the tomato, reported that figures of various workers on the pH

of ripe tomatoes range from 3.8 to 4.61. Hoffman, Krause, and Washburn (11) stated that acidity increases steadily during the period of fruit enlargement, and most rapidly as the fruits approach full size, but decreases during the ripening process. They did not report the pH of the fruits at various stages of maturity.

In the present investigation, tomatoes of various ages were macerated individually in a Waring Blendor and portions of this material were used to determine the pH with a Beckman pH Meter. In some tests certain sections of individual fruits were blended with a mortar and pestle and the pH determined in a similar manner.

Tomatoes less than 25 days old have a pH between 4.7 and 5.05. During the subsequent development there is a slow decrease in pH which lasts 20 to 30 days depending on the variety. This is followed by a sharp decrease to a point between pH 3.9 and 4.2 just prior to the development of red color

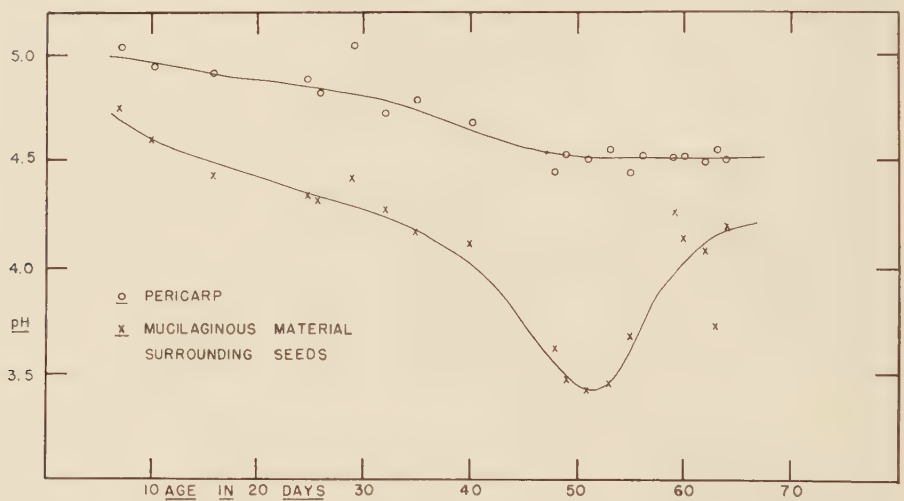

FIG. 3. The pH of the pericarp and the mucilaginous material surrounding seeds of Early Baltimore tomatoes of various ages.

in the fruits. The pH rises as the red color deepens so that mature tomatoes are between pH 4.2 and 4.6. There seemed to be slight consistent variations between the two varieties used but in the present work these differences were considered too minor to enter into the problem and could not be correlated with any differences in the amount of anthracnose.

Since the histological investigations demonstrated that the anthracnose fungus is confined mainly to the outer layers of the green fruits, the pH of various sections of Early Baltimore fruits was determined. The pericarp of the green and ripe fruits was found to have a consistently higher pH than the mucilaginous material around the seeds (Fig. 3). The pH of the pericarp drops slowly during the development and maturation of the fruit. On the other hand, the mucilaginous material surrounding the seeds shows a marked decrease in pH as the green fruits approach full size. During the

change from green to red-ripe the pH of this material rises and approaches that of the pericarp. This would indicate that the changes in pH noted in the whole fruits during maturation are the result of the changes in the interior of the fruits and not in the outer layers. It is in these outer layers that the anthracnose fungus remains apparently latent following penetration of the cutin layer. The inner walls of the carpels and the placental tissue have a pH between the two values presented in figure 3.

A series of cultural studies was run to determine the growth of *Colletotrichum phomoides* on media with a wide pH range. The fungus was grown on potato-dextrose agar containing 2.5 gm. of K_2HPO_4 per liter. The pH was adjusted to various levels by aseptic addition of 50 per cent citric acid

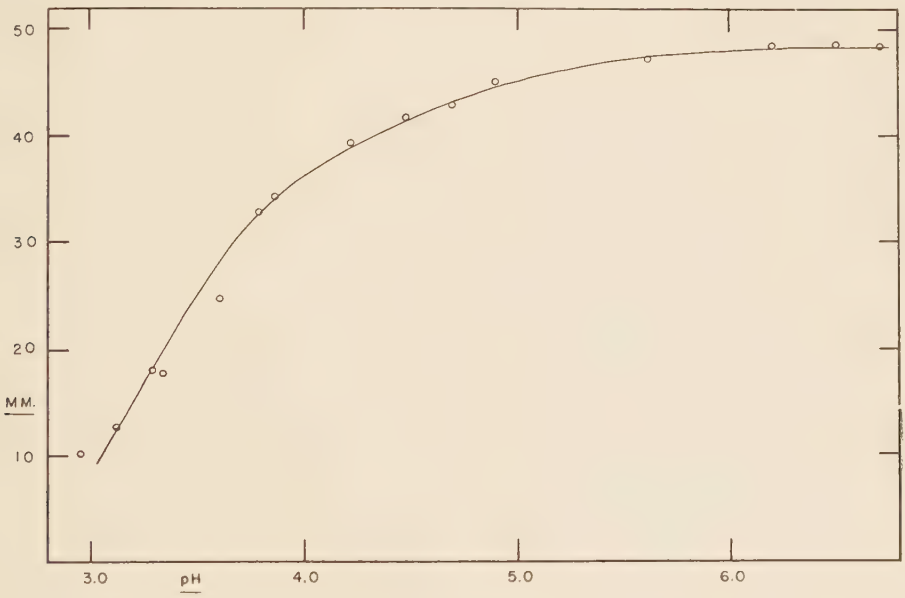

FIG. 4. The relation of pH to the growth of *Colletotrichum phomoides* on potato-dextrose agar. Diameter of colonies after five days at 80° F.

just before the agar was poured into Petri dishes. While the plates were being poured the pH of each medium was determined with a Beckman pH Meter. The agar was inoculated with a disc 1 mm. in diameter from the edge of a young colony of *C. phomoides*. The cultures were incubated at 80° F. for five days. The size of the colonies was determined by averaging the extreme diameters.

The pathogen grows well in culture within the extremes of pH found in tomato fruits (Fig. 4) and is not markedly inhibited unless the pH is lower than that found in green or ripe fruits. The range of pH found in the pericarp of tomatoes, pH 4.5 to 5.0, appears to be admirably suited to the growth of *Colletotrichum phomoides*.

It is apparent that the changes in pH which occur in the fruits during ripening do not influence directly the development of anthracnose on ripe

tomatoes. The inoculation studies demonstrated that *Colletotrichum phomoides* may occasionally penetrate at the style of the very young fruits and develop in the interior. In this stylar infection, the pericarp, and in particular the hypodermis and epidermis, are the last tissues to be invaded by the fungus. The inner tissues of the green tomatoes have a pH at which minimum development of the fungus would be expected. For this reason there must be factors in the pericarp other than pH which inhibit the growth of the fungus in green fruits.

Since the anthracnose fungus is confined to the epidermis and hypodermis during the latent stages of infection and no attempt was made to separate these tissues from the remainder of the pericarp, it is obvious that the pH of the immediate environment of the fungus has not been determined.

DISCUSSION

The present studies show that the pathogen causing tomato anthracnose is capable of penetrating the cuticle of green as well as ripe tomatoes, although lesions are produced only on ripe fruits. In green fruits the fungus remains latent until ripening begins. The fungus is able to push between the cell wall and the cutin layer to a limited extent but there is no evidence that it is capable of dissolving or penetrating the wall while the fruit is still green. The growth of the fungus in green fruits may be restricted by the composition of the cell walls. These cell walls, in addition to cellulose, are composed of protopectin which is partially converted to pectin in the ripening process. Simmonds (15) suggested that the latent condition of the banana anthracnose fungus in green fruits may be caused by the inability of the fungus to attack the protopectin of the cell walls. During ripening the protopectin is converted to soluble pectin which the fungus is presumably able to attack. Le Crone and Haber (12) have shown that protopectin is converted to soluble pectin during ripening of tomato fruits.

Sando (14) discussed the process of ripening in the tomato and pointed out that the most striking change which occurs is that undergone by the carbohydrates. Sugars increase during the maturation of the fruit and starches decrease during the same period of time. These changes, however, can not be expected to affect drastically a fungus which exhibits very little selectivity in regard to the source of carbon in its nutrition.

The relative amount of moisture is probably the controlling factor influencing infection under field conditions since the fungus can infect the fruits over a wide range of temperatures. The fungus can continue development in the ripe fruits over a similar wide temperature range. Therefore, if the fruits are infected in the field, little can be done by controlling storage temperatures to prevent the development of lesions as the fruits mature. Treatment of the harvested fruits with fungicides prior to storage can be expected to give little appreciable control of anthracnose since the fungus is latent beneath the cutin layer.

Wounds occurring naturally or produced in handling can not be considered an important factor in the development of this disease. Cultural practices which reduce wounding or breeding work to minimize cuticular cracking can not be expected to produce reductions in the amount of anthracnose. The pathogen penetrates the uninjured cuticle with ease and it is likely that this type of infection is responsible for serious outbreaks of the disease.

Since the fungus is capable of remaining latent in green tomato fruits, effective control with fungicides is dependent upon good coverage of each fruit throughout the entire period of its development on the vine. Sprays and dusts applied at the time the fruits are ripening may give a slight reduction in the amount of anthracnose but such treatment can not be expected to affect the latent infection which may already be present in the fruits.

SUMMARY

A study was made of some of the factors related to infection of tomatoes by the anthracnose fungus, *Colletotrichum phomoides*, using greenhouse-grown fruits.

When the pathogen was introduced through wounds in fruits on the vine, infection was readily obtained on large green or mature fruits. Infection was obtained on unwounded areas of tomato fruits less than 20 days old but not through wounds on these fruits.

Unwounded tomatoes were susceptible to infection from the time the fruits were 10 days old until maturity. The susceptibility to infection increased with the age of the fruits. The fungus, in green fruits, remained latent until the fruits ripened and produced typical lesions at that time.

Detached, mature, unwounded tomato fruits were readily infected through a wide range of temperatures below 90° F. Lesions were produced most rapidly at 80° F.

Colletotrichum phomoides penetrates the cuticle of the fruit by means of a penetration tube which grows from the lower side of the appressorium. The infection tube in green fruits swells slightly on contact with the cell wall but remains latent between the cell wall and the cutin layer. As the fruits ripen the fungus enlarges and produces swollen, inter- and intracellular hyphae in the hypodermis. Upon contact with the parenchyma cells the fungus develops many fine hyphae which grow rapidly through the walls and cell contents. Microscopic cracks in the cuticle are not believed to be a factor in infection.

There is no apparent relation between the pH of the fruits during ripening and the development of lesions. The fungus grows well within the ranges of pH found in tomatoes.

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